

THE REACTIONS OF INSECTS TO LIGHT

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THE REACTIONS OF INSECTS TO LIGHT

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ADAPTATION VERSUS EXPERIENCE AS AN EXPLANATION OF MODIFICATION IN CERTAIN TYPES OF BEHAVIOR¹ (CIRCUS MOVEMENTS IN NOTONECTA)

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TWO FIGURES

INTRODUCTION

Insects with one eye covered, when exposed to light, usually turn continuously toward the functional eye if positive, and away from the functional eye if negative to light; i.e., they perform circus movements. Exceptions to this generalization were found by Axenfeld ('99) and Rádl ('03) on *Calliphora vomitoria*, by Holmes ('05) on *Ranatra* and *Notonecta*, by Carpenter ('05) on *Drosophila*, by Brundin ('13) on the terrestrial amphipods, by Dolley ('16) on *Vanessa antiopa*, by Minnich ('19) on the honey bee, and by Mast ('23) on *Eristalis*.

Rádl found that *Calliphora* larvae move in practically a straight line when they have one eye blackened as they do with both eyes functional. Carpenter found that *Drosophila* with one eye blackened moves toward a source of light without the performance of circus movements. No explanation was given but it was pointed out that the response is directly opposed to the theories of orientation current at that time.

Holmes showed that *Ranatra* and *Notonecta*, with one eye covered, at first perform circus movements in creeping toward a light, but that, after repeated trials, the behavior is modified

¹I desire to thank Dr. S. O. Mast, of Johns Hopkins University, Baltimore, Maryland, for help and advice in the preparation of the manuscript.

and the animal creeps directly toward the light. Holmes believed this phenomenon to be due to a dropping of useless movements or the suppression of movements which tend to carry it away from the light. In short, he believed that the insects by repetition gain experience which results in the elimination of circus movements; i.e., that they learned to go directly toward the light by repeated trials.

Dolley brought the subject a little nearer solution when he pointed out that modification in circus movements depends upon the direction of illumination. He found that if the insects with one eye covered are illuminated from above there is no modification of circus movements, but that if they are exposed in a well-defined beam of light on a dull black background, there is modification in three respects: 1) decrease in the number of circus movements made; 2) decrease in the angle of deflection; and, 3) increase in the promptness with which they orient on reaching the edge of the beam. He gave no explanation except that he suggests that the modification is due to experience, i.e., the insect learns to go in a straight course by performing the same actions again and again. On the basis of this explanation, it is then quite pertinent to inquire why the insect learns to go in a straight course, i.e., reduces the number of circus movements made, when it is in a well-screened beam of light, while it does not learn to decrease the circus movements when illuminated from above.

One thing seems clear, that is, that if the external conditions remain constant and modification of circus movements occurs, it must be owing to a change in the internal factors. It is, then, in the elusive internal factors that we must look for an explanation. It is the purpose of this paper more fully to analyze the modification in behavior observed in insects with one eye covered.

MATERIALS AND METHODS

The common aquatic hemipteron, *Notonecta undulata*, was chosen, for it is readily procured in adequate numbers, it reacts strongly to light and it performs definite circus movements.

The insect is about 16 mm. in length, with a blunt head and a slightly broader thorax, from which it tapers gradually to the posterior end. The eyes are large, uniform in shape, and generally reddish-brown in color. The legs have been considerably modified, the first two pairs for clasping, while the posterior pair has been greatly lengthened and is fringed with hair for swimming. In crawling, the hind pair of legs usually takes but little part in locomotion.

The most peculiar and striking feature in the behavior of *N. undulata* is found in the fact that when the animal swims the morphologically ventral surface is up (i.e., it swims on its back), but when it crawls on a solid substratum the dorsal surface is up. The insect is predaceous, feeding upon almost any hapless organism that it is able to overcome. Hungerford ('19) gives a fine summary of its habits, ecology, and life-history, and Bueno ('02, '05) has written on its behavior.

The experiments were performed in a dark room in light from a 150-watt Tungsten Mazda lamp, constant care being taken to prevent fluctuations in the current. The lamp was burned, base down in a light-tight box, $20 \times 30 \times 60$ cm., painted dead black inside and outside. A ground-glass plate, 4×6 cm., was inserted in one side of the box to act as a secondary source of light. The lamp was placed 50 cm. behind the ground-glass plate. This gave a fairly uniform source of illumination, 4×6 cm. The light from this source was so screened and adjusted that it produced a horizontal beam which at a point 60 cm. from it was 15 cm. wide. Scattered light was largely absorbed by the dead black walls of the dark room, the nearest upon which the direct beam impinged being 2.5 meters from the source.

In carrying out an experiment the procedure was as follows: One eye of each notonectid used was covered with a thick coating of asphaltum. After the asphaltum had dried, each insect was put into a dish, left in darkness for six to twenty-four hours and then placed in the center of the beam, 60 cm. from the source and allowed to travel until it reached a point 45 cm. from the source or until it moved out of the

beam; it was then allowed to crawl onto a strip of black paper, and was carried back to the starting-point, after which the test was repeated. Each of these individual tests was called a trial and will be so designated in this paper. The paths were kept for permanent record by following the insect with a pencil. The time for each trial, the temperature, and the number of circus movements were noted.

EXPERIMENTAL RESULTS

The dark-adapted insects with one eye covered invariably performed circus movements when placed in the beam. In doing this they moved, however, toward the source of light in a series of circles. As the number of trials increased the number of circus movements became less per trial and sometimes larger in size until eventually the animals went directly to the light. The results obtained in a typical series of trials are presented in figure 1. By referring to this figure, the following will be seen: The insect at first made numerous circus movements. After some few trials the circus movements began to disappear until, at the forty-third trial, the animal went in a straight line, and the circus movements were eliminated. Between the forty-third and forty-fourth trial, the animal was put under an inverted glass jar and left for one hour. Trials forty-three to forty-six demonstrate that circus movements did not reappear. Between the forty-sixth and forty-seventh trial the animal was exposed to darkness for fifteen minutes. Trials forty-nine to fifty-nine show that circus movements reappeared after exposure to darkness, but

Fig. 1 Tracings of paths made by a notonectid, illustrating the change in the courses as the number of trials increases. 1, 3, 7, etc., position of paths in the series. Interval between paths 43 and 44, one hour, during which the insect was left in the beam of light. Interval between paths 46 and 47, fifteen minutes, during which the insect was exposed to darkness. Interval between all other successive paths less than one second, the animal remaining in the beam. 1 to 43, paths showing decrease and final elimination of circus movements. 44 to 46, paths showing that circus movements are still absent after one hour's exposure in the beam. 47, path showing the reappearance of circus movements after fifteen minutes' exposure to darkness. 47 to 58, paths showing the re-elimination of circus movements during further trials.

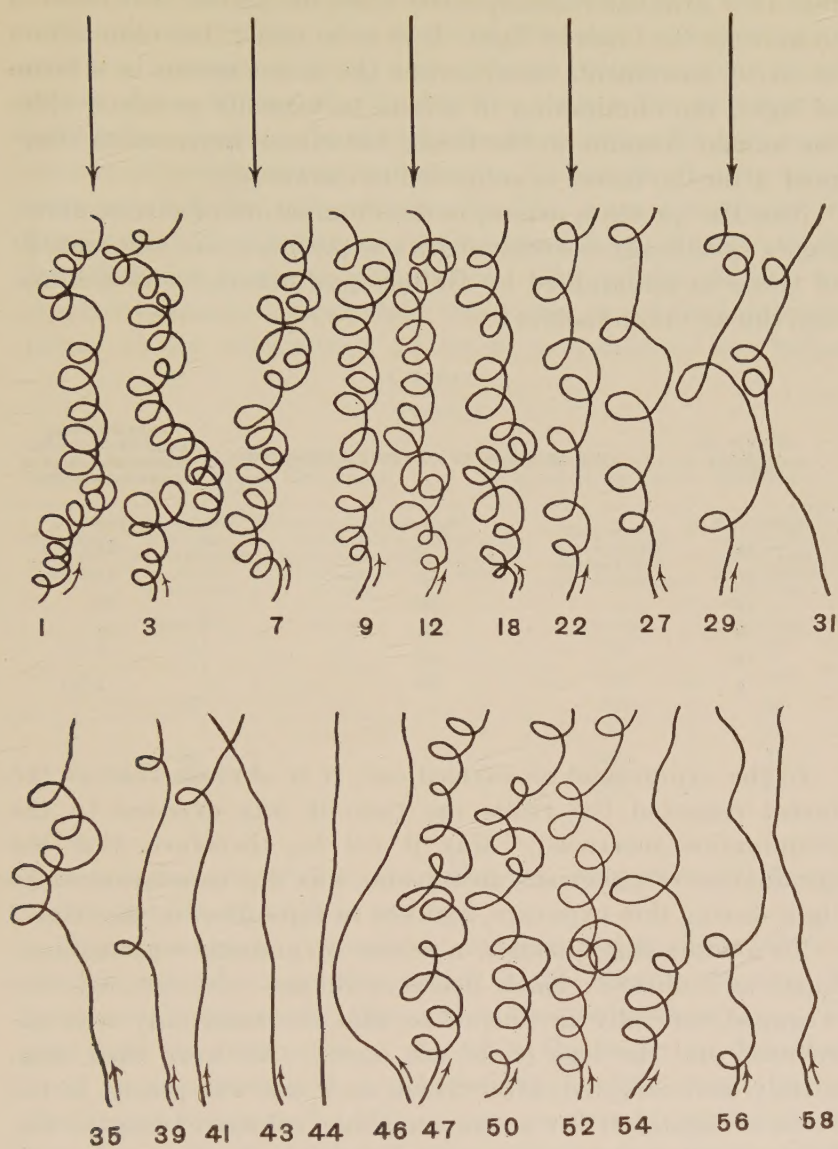


Figure 1

that they gradually disappeared when the animal was allowed to move in the beam of light. It is to be noted that elimination of circus movements occurs when the insect moves in a beam of light, the elimination of circus movements persists while the animal remains in the beam, but circus movements reappear after the insect is subjected to darkness.

Now the question arises, is the elimination of circus movements specifically correlated with experience, i.e., the number of trials as maintained by Holmes and others, or is elimination due to other factors?

TABLE 1

NUMBER OF ANIMALS TESTED	TIME OF EXPOSURE TO LIGHT BEFORE TEST	AVERAGE TIME REQUIRED BEFORE CIRCUS MOVEMENTS WERE ELIMINATED
	<i>Minutes</i>	<i>Minutes</i>
48	0	48
10	10	34
10	20	18
8	30	18
10	40	7
4	50	1(?)

In the experiment as carried out, it is obvious that as the insect repeated the trials the time it was exposed to the illumination increased. May it not be, therefore, that the elimination of the circus movements was due to adaptation to light during this exposure, and not to repetition in the trials?

To answer this question a series of animals was manipulated as follows: Each insect with one eye covered was wrapped carefully in tin-foil so that the head only was uncovered and the legs could not move. All were then completely dark-adapted, after which each one was placed in the beam of light, left for a time, and then released from the tin-foil and allowed to make repeated trials in the beam until the circus movements were eliminated. The results are presented in table 1.

A survey of this table shows, 1) that the insects not previously exposed to the light required repeated trials extending over an average of forty-two minutes before circus movements were eliminated; 2) that the longer the exposure to light before the test, the shorter the time during the test necessary to eliminate circus movements; 3) that the insects which were exposed for fifty minutes tended to go directly to the light without any trials, i.e., they tended to go directly to the light without previous experience. The results of this experiment seem to indicate that experience is not the important factor in the elimination of circus movements, but rather

TABLE 2

EXPOSURE TO LIGHT AFTER THE ELIMINATION OF CIRCUS MOVEMENTS			EXPOSURE TO DARKNESS AFTER THE ELIMINATION OF CIRCUS MOVEMENTS		
Number of insects tested	Time left in light after elimination of circus movements	Time required to reeliminate circus movements after exposure to light	Number of insects tested	Time left in darkness after elimination of circus movements	Time required to reeliminate circus movements after exposure to light
	<i>Minutes</i>	<i>Minutes</i>		<i>Minutes</i>	<i>Minutes</i>
6	15	0	14	15	11
			10	30	19
2	30	0	5	60	28
			8	120	34
3	60	0	10	180	39
			3	240	44

that it is the exposure to the light, i.e., adaptation of the eye to the light in which it is exposed.

If the change in response is actually due to light adaptation, it should obviously persist if the insects are kept in light and disappear if they are subjected to darkness. To test this, the insects were placed in the beam as described until circus movements were eliminated. They were left in the beam for various lengths of time or were exposed to darkness for various lengths of time and then retested immediately. The influence of light and darkness upon the persistence of the modification of behavior which causes the elimination of circus movements is shown in table 2.

It is to be seen in table 2 that circus movements, once eliminated, do not again appear as long as the insect is exposed to the light, but they reappear if the insect is exposed to darkness. If the elimination of circus movements is correlated with adaptation to light, it would be expected that the longer the exposure to darkness, the longer is the necessary time of exposure to light before circus movements are reeliminated. That this obtains can be ascertained by consulting table 2. At the end of four hours' exposure to darkness, it took the insect as long to eliminate the circus movements as it did to eliminate them in the first test. It thus seems clear that elimination of circus movements is due to

TABLE 3

NUMBER OF ANIMALS TESTED	EXPOSURE BEFORE TEST		EXPOSURE DURING TEST	
	Intensity of light	Time of exposure in hours	Intensity of light	Average time required for elimination of circus movements
				<i>Minutes</i>
3	100	2	25	2
7	50	2	25	1
5	25	2	25	2
10	10	2	25	19
8	0	2	25	36

changes in the eye produced by light adaptation rather than to experience.

If the elimination of circus movements is caused wholly or in part by adaptation, then the time required for the elimination of circus movements should depend upon the relation between the intensity of the light to which the insects are adapted before the test and that to which they are exposed in the beam during the test. In the following series of tests the animals were kept in a light of given intensity until they were completely adapted, then each animal was placed in a horizontal beam of light of different intensity and the time required for elimination of circus movements ascertained. The results obtained are presented in table 3.

From this table the following conclusions seem justified: The time required for the elimination of circus movements depends upon the intensity of the light to which the animals were exposed before the test. The less the difference in the intensity of the light to which they are exposed before the test and that to which they are exposed during the test, the less the time required provided the intensity of the former exposure is less than that of the latter exposure. If the light to which the insect is adapted before the test is equal to or higher than that to which it is exposed during the test, it at once tends to go toward the light without the performance of circus movements, but if it is lower the animal tends to perform circus movements.

If the elimination of circus movements in *Notonecta* is due to light adaptation of the uncovered eye, then specimens which are exposed to light after one eye has been dark-adapted and the other light-adapted should perform circus movements toward the eye which was dark-adapted. The results given by Holmes ('05) on *Ranatra* indicate that this does not obtain, but those obtained by Garrey ('17) on the robber-fly indicate that it does.

Dark-adapted *Notonecta* with one eye covered were exposed until circus movements were eliminated. The covering was then chipped from the covered eye and the animals tested immediately.

Contrary to the results found by Holmes, but agreeing with those of Garrey, *Notonecta* was found to perform circus movements toward the dark-adapted eye (the previously covered eye) after the covering was chipped off. The length of time before the circus movements were eliminated is shown in table 4.

Inspection of this table shows that it takes nearly as long to eliminate circus movements when one eye is dark-adapted and the other light-adapted as it does when both eyes are dark-adapted but one is covered. However, it will be noticed that in five out of the six animals tested there was a shorter time of adaptation in the second eye than in the first. This

seems to indicate that the covered eye was not completely dark-adapted when the covering was removed. The asphaltum came off in quite large sheets; these sheets were examined under the microscope and found to be opaque. In some specimens cracks in the asphaltum were discovered, but all these were discarded.

DISCUSSION

It has been demonstrated above that the behavior leading to the elimination of circus movements in *Notonecta* is due to light adaptation, and not to experience. It remains now to consider the question as to how light adaptation operates in this modification of behavior.

TABLE 4

DESIGNATION OF INDIVIDUALS	TIME REQUIRED FOR ELIMINATION OF CIRCUS MOVEMENTS—ONE EYE COVERED AND THE OTHER DARK-ADAPTED	TIME REQUIRED FOR ELIMINATION OF CIRCUS MOVEMENTS AFTER COVER REMOVED; ONE EYE DARK-, OTHER LIGHT-ADAPTED
	<i>Minutes</i>	<i>Minutes</i>
a	43	41
b	39	35
c	45	40
d	37	41
e	44	40
f	46	45

Axenfeld ('99), Holmes ('05), Mast ('11, '23), Garrey ('17), and Yagi ('28) found, in various orders of insects, differences in the sensitiveness of different regions of the eyes. In an anteroposterior direction, Mast ('23) showed that there were at least three different responses given, depending upon the region of the eye stimulated. In *Eristalis* with one eye covered, he found the animal turned toward the light, i.e., toward the covered eye if the light stimulated the anterior inner edge of the eye, that it went directly toward the light without turning if the light stimulated the anterior part of the eye, and that if the light stimulated the lateral part of the eye the animal turned toward the functional eye. This is illustrated in figure 2.

It is well known that light adaptation causes a great decrease in the sensitivity of the eye. It is perhaps needless to say that in all experiments with light there is some reflection from the background. Owing to this reflection, an animal when placed in the beam received light in all parts of the eye, a high intensity directly from the source and much lower

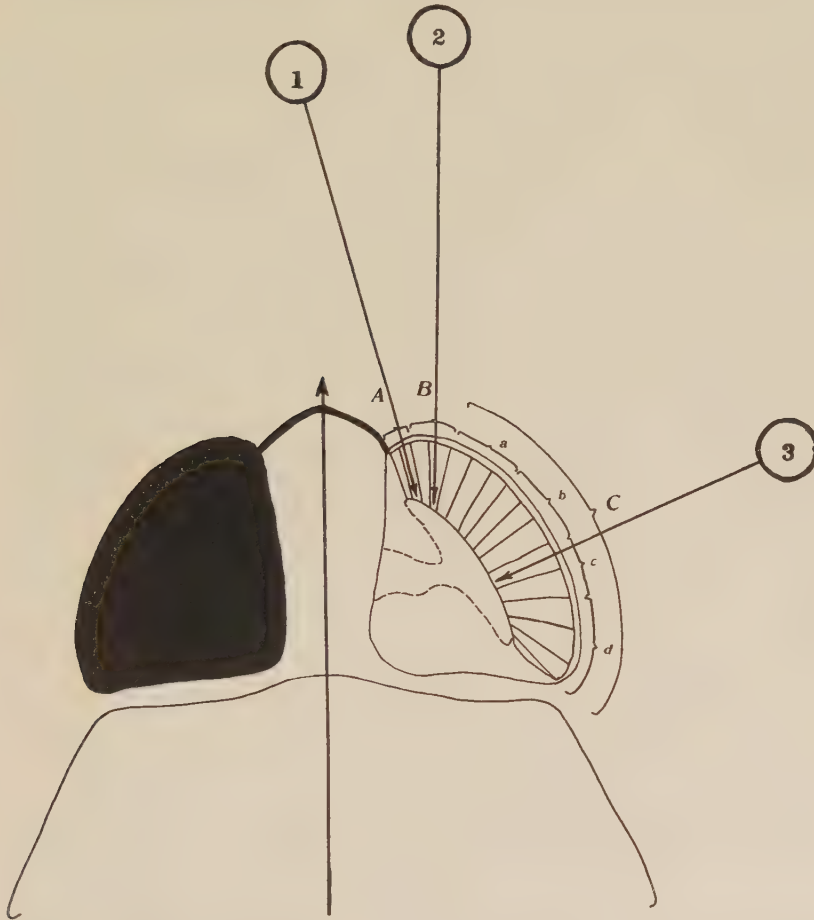


Fig. 2 Diagram showing how reaction to light is related to the part of the eye stimulated in an insect with one eye covered. 1, 2, 3, successive positions of light; arrows indicate effective rays and the part of eye stimulated. Light at 1 causes stimulation of area A and turning toward the covered eye; light at 2 causes stimulation of area B and no turning; light at 3 causes stimulation of area C and turning toward the functional eye.

intensities reflected from the background. The elimination of circus movement can be explained on the following assumptions.

When first put into the beam, the insect does not stop turning when in its circus movements it reaches a position in which it faces the light since the light reflected from the background striking the posterior ommatidia causes a continuation of turning.

During the course of the circus movement the posterior ommatidia are exposed to the full illumination of the light and become somewhat light-adapted. This causes a decrease in the sensitivity until eventually the reflected light falls below the threshold for stimulation. The light source is now the only effective source of stimulation. The animal turns until it is facing the light source and goes to the light without the performance of circus movements; the light striking the posterior ommatidia is below the threshold for stimulation and thus causes no stimulation resulting in circus movements. If this obtains, modification is due to the process of light adaptation rendering the posterior ommatidia so insensitive that the reflected light received by them when the animal is facing the light is below the threshold for stimulation.

In an insect with one eye covered which is oriented to the light, loss of circus movements would, according to this explanation, only occur if the light stimulating the posterior parts of the eye is of such an intensity that it is below the threshold when the eye is light-adapted.

Dolley ('16) found that *Vanessa* with one eye covered modified its behavior in a well-screened beam of light in the dark room by eliminating circus movements and going in a straight course, but that in front of a window, a large light source, circus movements were performed continuously. In light from above, the so-called non-direction illumination, there has been no report of loss of circus movements with exposure or experience, although much work has been done. For example, Garrey ('18) found that the robber-fly did not modify its circus movements on a white background during

seven to eight days or until it died, and I have data (which will be presented subsequently) to show that circus movements depend upon the size of the light source.

According to the above theory, this persistency of circus movements may be assumed to be due to the fact that illumination falling upon the lateral and posterior ommatidia never falls below the threshold; and if this is true, it is to be expected that, though there may be a change in the degree of deflection in circus movements, there will never be a complete loss of them. Such conditions exist, if the intensity of the light reflected is large, as from a white surface; if the source of light is of such a size as to stimulate the lateral part of the eye even when the insect is oriented to the light as from a large light source; or if the light is so placed that the lateral and posterior ommatidia will be stimulated irrespective of the size of the source, e.g., light from above.

There can be no doubt, however, that habit and habit formation do cause modification in behavior (Holmes, '05, p. 336; Wodsdalek, '11); but in view of the fact that in adaptation we have an explanation of the elimination of circus movements in an insect with one eye covered, which not only does all that other explanations do, but correlates facts hitherto unexplained, it can be assumed that experience is not involved in this phenomenon.

SUMMARY

1. *Notonecta undulata* with one eye covered usually performs circus movements in a beam of light.

2. Circus movements are eliminated in a well-defined beam of light if a number of trials are made or if the animal is merely exposed in the beam without making circus movements.

3. After circus movements have been eliminated in a beam, this modification persists as long as the insect remains in the beam, but it disappears if the insect is subjected to darkness for some time.

4. The time before circus movements are eliminated in a beam of light is correlated with the time and intensity of light of previous exposure.

5. When one eye is dark-adapted and the other light-adapted, the insect performs circus movements toward the dark-adapted eye, but they are eventually eliminated.

6. The elimination of circus movements is probably due to light adaptation rather than to experience. The process involved consists in light adaptation causing such a decrease in the sensitivity of the eye that illumination effective in causing circus movements falls below the threshold of stimulation.

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SOME FACTORS INVOLVED IN THE REACTION OF INSECTS TO CHANGES IN LUMINOUS INTENSITY. SHOCK REACTIONS IN *DINEUTES ASSIMILIS*¹

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ONE FIGURE

Dolley ('16), working on *Vanessa antiopa* with one eye covered, observed that specimens which were oriented in a beam of light turned sharply toward the functional eye when the intensity of the light was suddenly increased and in the opposite direction when it was suddenly decreased, but gave no response if the intensity was slowly changed. This response, therefore, appears to be dependent upon the rate of change in the magnitude of the stimulating agent and is consequently in accord with responses sometimes designated 'shock reactions.'

Experiments described in the following pages concern the questions of the factors involved in responses similar to these.

MATERIAL AND METHODS

Specimens of *Dineutes assimilis* (Gyrinidae, Coleoptera) were used throughout the series of experiments; they orient well in a beam of light and are favorable in other respects.

One of the most conspicuous features in the morphology of the gyrids is the division of each compound eye into two parts; each animal has apparently two pairs of compound eyes, a dorsal and a ventral pair.

¹ This work was carried out under the direction of Prof. S. O. Mast. I desire to express my thanks and appreciation to him for helpful suggestions, especially in the preparation of the manuscript.

In all experiments the two parts of the eye on the left side were covered with a mixture of black Duco paint and asphaltum varnish. The experiments were carried out in a dark room in a beam from a 150-watt Mazda lamp. The lamp was enclosed in a light-tight box having a rectangular opening in one side, covered with a piece of ground-glass, 1×1.5 cm. The beam was so screened that it was 9 cm. wide at a point 100 cm. from the ground-glass, and its edges were sharply defined. Wratten neutral-tint filters were inserted across the beam to change the intensity. The experimental animals were placed on a sheet of medium gray photographic paper and exposed in the beam of light 100 cm. from the source. The photographic paper was on a level horizontal platform at the same height as the lower edge of the ground-glass screen.

RESULTS

When first exposed in the beam of light, the animals performed circus movements toward the functional eye (fig. 1, A). After several trials, they oriented and without performing circus movements crept diagonally across the beam until they came to the edge; then they turned directly toward the source and continued near the edge of the beam (fig. 1, B). If the intensity of the source was suddenly increased or decreased while they were moving diagonally across the beam, they turned respectively away from or toward the source (fig. 1, C). If, however, the intensity was changed slowly, no response occurred, showing that the reactions in *Dineutes* are similar to those described by Dolley (*loc.cit.*) for *Vanessa*.

How does light act to produce these reactions? What conditions underlie them? It is evident that when the intensity of the source is increased, the intensity of the light reflected from the background is increased proportionally. The reaction may therefore be due either to the increase of light received directly from the source, or to the increase of light received from the background, or to the increase in the light received from both the source and the background, or to some relation between these. It was therefore necessary to devise

a method by which the intensity of the light coming directly from the source could be changed suddenly while that from the background remained constant.

This was done as follows: Sheets of photographic paper were exposed in such a way that, after development, one-half of every sheet was the same in density, while the other half differed, being denser in some, less dense in others. A comparative measure of the light reflected from each half of each sheet was secured as follows: A sheet was placed on the level platform, described above, and in the beam. With a camera suspended 25 cm. above the platform, one-half of the sheet was photographed with an exposure of one second; then the other half was photographed ten times in succession with the same exposure period (one second), but each of the ten exposures was made with a different known light intensity. All the negatives so secured were developed and fixed simultaneously. Thus one negative was obtained of one-half the sheet and a series of ten negatives of the other half. The one was then compared with each of those in the series of ten and a match found having the same density. The relation between the intensities of light by which the matched negatives were taken was assumed to be the relation between the coefficients of reflection of the two halves of the prepared sheet. By this process, the coefficient of reflection was found for all the sheets and their comparative value ascertained. Two sheets were now selected, the two halves of which had coefficients of reflection related as X and $X/10$, and X and $10X$, respectively. These sheets will be called sheet I and sheet II.

One of these sheets was now placed horizontally in the beam and so arranged that one-half of the field had a darker background than the other; that is, the sheet was so arranged that the lighter gray was on one side and the darker gray on the other, with the line of demarcation between the grays parallel to the direction of the rays. Under these conditions, when an insect, in moving on this background diagonally across the beam, creeps from one shade to the other, the

intensity of the light reflected from the background upon it changes, while the intensity of the light striking it from the source remains the same.

A dark-adapted insect with the eyes on the left side covered was now placed in the beam on a uniform gray background

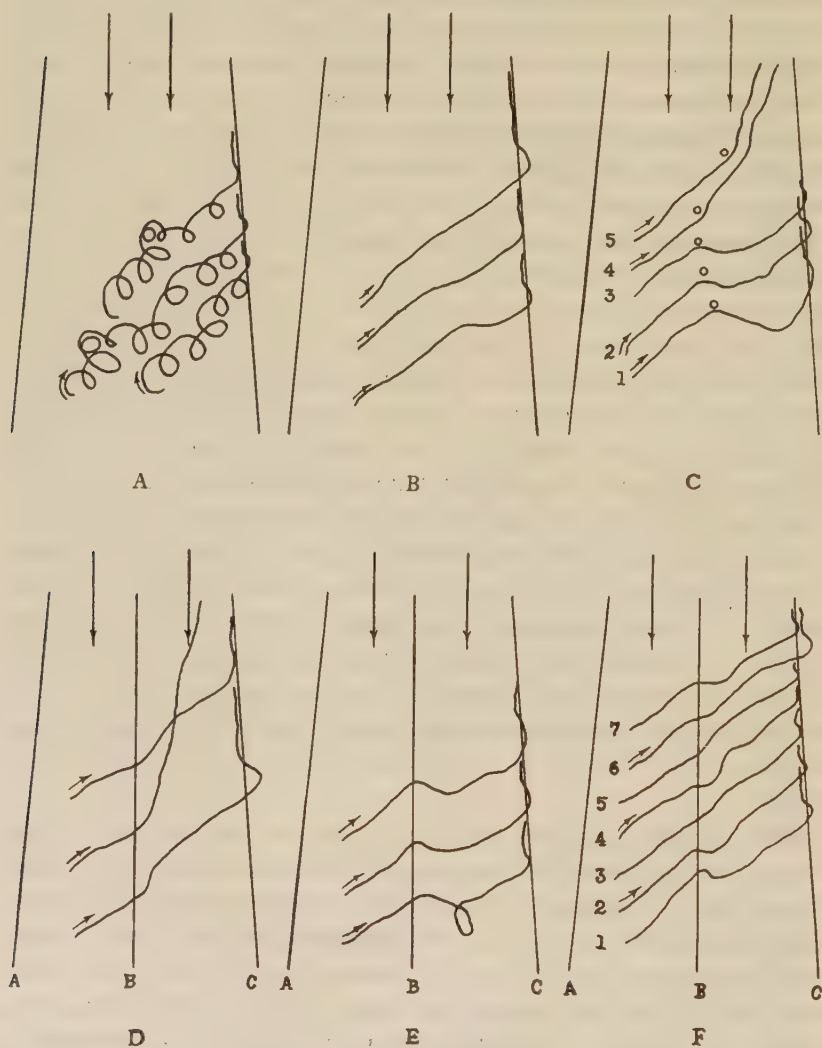


Figure 1

and kept there until all circus movements had disappeared. One of the prepared sheets (sheet I) of the photographic paper was then substituted for the uniform gray one and arranged so that the lighter half was on the left side; the insect was placed on the lighter half at the left edge of the beam. It at once oriented diagonally in the beam and then took a straight course until it came to the edge of the darker half of the sheet used as a background; at this point it swerved sharply toward the source, markedly decreasing the angle that the path made with the direction of the rays

Fig. 1 Path made in a beam of light by *Dineutes assimilis* with left eye covered. Divergent lines, margin of beam; large arrows, direction of illumination; small arrows, direction of creeping of insect.

A. Immediately after it was placed in a beam of light on a gray background. Note that circus movements were made toward the functional eye until the edge of the beam was reached, after which the insect moved directly toward the source.

B. After being in the beam for a few minutes. Note the elimination of circus movements, the diagonal path across the beam, and the turning toward the source at the margin of the beam.

C. Paths showing reactions to a sudden change of intensity after the circus movements were eliminated. Circles designate points on path at which intensity was changed. Paths 1, 2, 3; intensity increased ten times. Note that insects swerved sharply away from the source. Paths 4, 5, 6; intensity decreased to one-tenth. Note that insects turned sharply toward the source.

D. Paths showing responses due to a sudden decrease of intensity of light reflected from the background without any change in the intensity of light from the source. A-B, background with a coefficient of reflection X; B-C, background with a coefficient of reflection of X/10. Note that when the insect reached the darker background, it turned sharply toward the source.

E. Response due to a sudden increase of intensity of light reflected from the background without any change in the intensity of the light from the source. A-B, background with a coefficient of reflection of X; B-C, background with a coefficient of reflection of 10X. Note that when the insect reached the lighter background, it turned sharply away from the source.

F. Paths made during a sudden increase of intensity of light from the source, without any change in the intensity of light reflected from the background. A-B, background with a coefficient of reflection of X; B-C, background with a coefficient of reflection of X/10. When the insect reached a point on the line b, the light from the source was increased ten times. In paths 1, 2, 4, and 7 the paths turn suddenly away from the source; the light was increased too soon. In path 6 the insect turned sharply toward the source; the light was increased after the insect crossed the line. In paths 3 and 5 the paths show no deviation; the light was increased at the precise moment that the insect passed the line B-D.

(fig. 1, D). In this way each of fourteen insects was tested ten times. In all similar results were obtained.

The experiment was repeated with sheet II, but in this test the darker half of the sheet was placed on the left side of the beam. When the insect was placed in the beam as before, it oriented and crept diagonally until it came to the lighter background; at that point it suddenly turned from the source of light, increasing the angle that its path made with the direction of the rays in the beam (fig. 1, E).

These responses are precisely like those resulting from a sudden decrease or increase from the source. Therefore changes in intensity of light from the background rather than changes in intensity of the source appear to be the deciding factor in these reactions.

To test this conclusion further, experiments were made to find the resulting response when the intensity of light from the source was suddenly changed while the intensity of light reflected from the background remained constant. Two methods were used.

In the first, sheet I was placed as described above, i.e., with the lighter shade on the left side of the beam, so that the background on the left reflected light which was ten times as intense as that reflected from the background on the right side. An insect with the eye on the left side covered was now placed in the beam as described above. It started diagonally across the beam; as soon as it reached the darker background, the intensity of the source was suddenly increased ten times. In this way the intensity of the light reflected from the background to the eye of the insect remained constant, but the intensity of the light impinging upon the eye directly from the source increased ten times. In a large number of trials made in this way there were a few in which no change in direction of movement occurred when the intensity of light from the source was increased (fig. 1, F, paths 3 and 5). In all the rest the insect turned either away from or toward the source of light (fig. 1, F). In these it was quite apparent, however, that the turning was due to

the fact that the intensity was changed too soon or not soon enough.

In the second method used to test the influence of sudden changes of intensity from the source with constant intensity from the background, the photographic paper and its support used in the preceding tests were replaced by a ground-glass plate. Under the glass plate a lamp was so placed that it transmitted light of low intensity through it. In these tests the light from the background came from two sources: that reflected from the surface of the plate and that transmitted through the plate.

The apparatus was standardized as follows: The intensity of light in the horizontal beam was increased tenfold, which increased the reflection from the plate; then the intensity of the light transmitted through the plate was reduced until the total amount of light coming from the background (transmitted plus reflected light) was the same as it was before. Then a method was devised by which the two intensities could be changed simultaneously in such a way as to change the intensity of light in the beam and at the same time keep the intensity of light from the background constant.

An insect which had the left eye covered, and in which circus movements had disappeared, was now placed on the ground-glass plate near the left edge of the beam. The insect oriented and started to move on a straight path diagonally across the beam. When it had reached the middle of the beam, the intensity of the horizontal beam of light was suddenly increased ten times and at the same instant the intensity of the transmitted light was suddenly decreased so as to keep the intensity of light coming from the background the same as it was before. The insect continued on its path without change of direction, i.e., there was no reaction. Only four insects were tested, but with each results like those presented were obtained.

These results seem to prove conclusively that the shock reactions described are due to sudden changes in the intensity of the light reflected from the background. The question now arises as to how the reflected light produces these reactions.

DISCUSSION

Why changes in the intensity of the light received directly from the source do not cause a reaction while changes in the intensity of that reflected from the background do, can only be inferred. The light received directly from the source enters the eye of oriented specimens near the anterior surface; and it may well be that the intensity of light entering this part of the eye under the conditions which obtained in the above experiments is so great that there is no discrimination between the highest and the lowest intensity received.

In discussing the question as to how reflected light produces these reactions it is expedient first to account for the elimination of circus movements and for the resulting diagonal orientation.

As is well known, the insect eye is composed of a large number of ommatidia arranged radially with the long axis at right angles to the periphery of the eye, and there is considerable evidence that only those rays entering the ommatidia parallel to their long axes are effective in producing stimulation (Taliaferro, '20; Mast, '23). Mast ('12, '23) further demonstrated that there is in insects a differential response to a localized stimulus in the eye. If one eye is covered and the anterior inner part of the other eye is stimulated, they turn toward the covered eye; if the anterior part is stimulated, they do not turn; and if the lateral and posterior parts of the eye are stimulated, they turn toward the uncovered eye. As stated above, specimens of *Dineutes* with the eyes on one side covered, when first placed in a beam of light, perform circus movements for a time; then they take a straight course. The mechanism involved in the elimination of circus movements was considered previously (Clark, '28) and the following conclusions formulated.

Light enters the insect's eye not only from the source, but also from the background. The light reflected from the background strikes all parts, including the lateral and posterior parts of the eye from all angles. Mast ('23) and, later, Dolley and Wierda ('29) showed that the lateral and the posterior

parts of the eye are more sensitive than the anterior parts and that stimulation of these parts results in turning toward the side stimulated. The stimulation of the ommatidia by light from the background causes the insect to turn toward the functional eye continuously, i.e., causes circus movements. As the insect performs circus movements, all parts of the eyes are exposed to light directly from the source and this is much stronger than that received from the background. This brings about light adaptation, i.e., a decrease in the sensitivity of the eye and a rise in the threshold of stimulation. This continues until the light reflected from the background (causing circus movements) falls below the threshold of stimulation for circus movements. As soon as this obtains, circus movements cease and the insect follows a straight path diagonally² across the beam. If these conclusions are valid, it appears evident that the diagonal course is the result of a balance between the effect of the stimulus from the source, tending to turn the insect toward the source, and the effect of the stimulus from the background, tending to turn it away from the source.

It has been shown, as stated above, that when the intensities of the light from the source and the background are proportionally and simultaneously changed, the insect does not deflect in its course, provided the change of intensity is gradual; but that if it is rapid, there is deflection and that this deflection in the direction of the path of the insect is due to change of intensity of the light reflected from the background, not of that received directly from the source. How, then, does reflected light produce the deflection, i.e., the reaction?

If the diagonal path is due to a balance between the effect of the light directly from the source, tending to cause the insect to turn toward the source, and the effect of that

² The insect takes a diagonal path only if it is on a gray background. If a white background is provided, it makes circus movements continuously; if a black one, it goes directly toward the light. This indicates that the diagonal path is the resultant of balanced stimulation.

reflected from the background, tending to cause it to turn from the source, it is evident that if the effect of the latter is decreased the insect will turn toward the light and if it is increased it will turn from the light. If this is true and if the assumption is valid that the elimination of circus movements and the taking of a diagonal course are due to the progression of light adaptation in some of the ommatidia of the posterior portion of the eye to such an extent that they are no longer stimulated, a sudden increase in the intensity of the reflected light will stimulate some of these posterior ommatidia, resulting in a turning from the light, i.e., in a reaction; and a sudden decrease in the intensity of the reflected light will result in a decrease in the number of ommatidia stimulated in the posterior portion of the eye and in a turning toward the source of light—likewise a reaction.

When the intensity is changed slowly, no reaction occurs. This may be accounted for by assuming that adaptation keeps pace with the change in intensity so that there is no change in the number of ommatidia stimulated.

The intensity of the reflected light can obviously be changed either by changing the intensity of the light at the source or by changing the character of the background. For example, when the insect passes from a light to a dark background or when it reaches the margin of the beam, the intensity of light reflected from the background is much reduced. This results in a turning toward the source.

The hypothesis advanced here to account for the above type of reaction not only correlates the facts as they are known, but serves indirectly as further evidence that the modification of circus movements is due to a process of light adaptation.

SUMMARY

Specimens of *Dineutes* with one eye covered, when placed in a beam of light on a suitable background, perform circus movements for a time, then go in a straight path diagonally across the beam. If, after the insects are oriented, the light is rapidly increased, they turn sharply from the source; if it is suddenly decreased, they turn sharply toward the source. These responses depend upon light reflected from the background.

The elimination of circus movements is probably due to light adaptation progressing to such an extent that some of the ommatidia of the posterior portion of the eye are no longer stimulated after orientation. If the intensity is now increased rapidly, some or all of these ommatidia are probably stimulated and the insect turns from the source of light. If the intensity is decreased rapidly, more of the ommatidia probably cease to be stimulated and the insect turns in the opposite direction.

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MODIFICATION OF CIRCUS MOVEMENTS IN INSECTS ¹

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FOUR FIGURES

INTRODUCTION

Insects with one eye covered may cease to perform circus movements after being exposed to light for some time. It was shown (Clark, '28) that light adaptation probably caused certain ommatidia to be thrown out of function. It remains to ascertain why, in some cases, insects do not perform circus movements when one eye is covered even though they are not light adapted (Rádl, '03; Carpenter, '05), or why, at other times they perform circus movements continuously, i.e., why light adaptation is ineffective in modifying circus movements.

This involves more than a simple study of circus movements. No matter what position the insects take in relation to the light, stimulation is asymmetrical and they should be caused to turn. The processes involved are probably the same as those in orientation, so an examination of the factors modifying circus movements may yield evidence concerning orientation itself.

Some evidence is available that circus movements can be modified, 1) by changing the intensity of light (Garrey, '18; Minnich, '19; 2) by changing the location of the stimulus in the eye (Dolley, '16; Minnich, '19; Mast, '23; Yagi, '28); and, 3) by subjecting insects with one eye covered to light for some time (Holmes, '05; Dolley, '16; Minnich, '19; Mast, '23;

¹ I am much indebted to Prof. S. O. Mast under whose direction the experiments described were made, for generous assistance and valuable criticism.

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Clark, '28). Some definite opinions have been advanced by the authors mentioned concerning the fundamental factors involved in circus movements. Likewise, a few suggestions have been made concerning their disappearance and modification. These will be considered later.

THE ORGANISM

Preliminary experiments early showed that *Dineutes assimilis* Aube was a happy choice of experimental material. It is almost indefatigable in its creeping toward a light, orients accurately and with precision, lives well in the laboratory, is very hardy, and is easily kept in large numbers.

Dineutes belongs to that family of coleopterous insects, the Gyrinidae, which can be seen very commonly in ponds and quiet waters swimming in zig-zag patterns on the surface. They are commonly called whirligig beetles, lucky bugs, coffee bugs, or apple bugs. Wilson ('23) gives an account of their life history, biology and habits.

The two posterior pairs of legs of *Dineutes* are considerably modified; the coxae are reduced; and the tibiae and tarsi are flattened to form a large propulsion surface. The two anterior legs are prehensile and in swimming are usually folded under the body. Out of water, they engage in locomotion and orientation with the remaining two pair assisting.

Each compound eye is divided, as in all Gyrinidae, into two separate portions, one being above and the other below the median lateral line (fig. 1). It has been suggested that the lower portions serve in under water vision and the upper in air vision. Miall ('03) points out, however, that the occurrence of divided eyes in some dragon flies, in *Adelotopus*—a carabid beetle inhabiting the bark of trees, and in some Diptera which never approach the surface of the water, casts some doubt upon the probable correctness of this notion.

Dineutes kept in the laboratory for use in this investigation was fed on various insects, small, freshly killed fish and small tadpoles. The two limiting factors in feeding *Dineutes* appear to be its inability to feed much below the surface and

its disinclination to feed upon animal food more than a short time dead. *Dineutes* was kept in good condition in laboratory aquaria for 9 months with no other attention than feeding animal food regularly.

On a solid substratum, the insects will follow a light for hours but they seem to be indifferent when swimming.

THE MODIFICATION OF CIRCUS MOVEMENTS BY CHANGING THE INTENSITY OF LIGHT

Dolley ('16) asserts that the rate of turning of *Vanessa* is approximately the same in all intensities above 0.02 m.c.

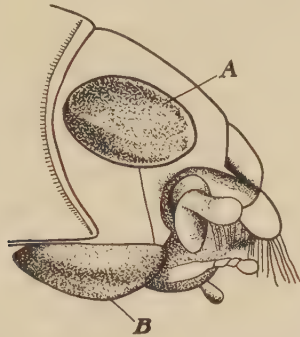


Fig. 1 Sketch of head of *Dineutes*, side view. A, upper portion of right eye; B, lower portion of right compound eye.

Garrey ('18) and Minnich ('19) maintain that the rate of turning in circus movements of the robber fly and the honey-bee, with one eye covered, increases as the intensity increases.

The following experiments show the relation between the luminous intensity and the rate of turning of *Dineutes* with one eye covered.

The apparatus used consisted of a light-tight box, a 150 watt Mazda lamp and a platform. The lamp was burned base upward in the box which was $30 \times 112 \times 12$ cm. The box contained two sheet metal screens with holes in the center 8 cm. in diameter. It was suspended 18 cm. above a dull black platform in the center of a dark room. The light from above produced on the platform a field of light, (non-directive)

16 cm. in diameter. Reflection, except that from the surface on which the insect moved, was very slight, owing to the fact that no direct light fell upon the surrounding walls and that these were at least 2 meters from the table. The intensity could be changed by inserting Wratten neutral tint filters across the beam.

The tests were made as follows: An insect was wrapped in a strip of lead-foil in such a manner that only the head was free. Then it was placed in a chamber which had been cooled to about 2°C. In a few minutes it became motionless, then it was put under a binocular and an opaque mixture applied so as to cover all the right eye. This hardened before the insect became active. It was now dark adapted for 6 to 8 hours, then put on a heavily smoked paper on the platform in the field of light produced by the vertical beam and left about a half minute, during which time it traced its path on the smoked paper. Then it was dark adapted for half an hour. After replacing the sheet of smoked paper containing the self-recorded path of the insect with another, the test was repeated, either in the same or a different intensity. Complete records were secured from twenty insects.

The results are presented in curve A, figure 2. The amount of turning in degrees per centimeter is plotted against the intensity. It is obvious that there was no great increase in turning with increase of intensity above 1.3-foot candles,³ but that below 1.3-foot candles the deviation decreases markedly with decrease of intensity.

Another experiment was made in essentially the same manner with the exception that a piece of ground glass was inserted across the opening of the light box so that it acted as a large secondary source. The results are shown by curve B, figure 2. This curve shows that the amount of turning increased with the intensity within larger limits than in the former experiment. A third experiment was performed in the

³ It was at this intensity that the curve flattened in the present experiment. This point is by no means fixed but depends upon the size of the source of light used.

same way as the first except that the black background was replaced by white paper. The results were essentially similar to those found in the second experiment (curve B, fig. 2).

By thus modifying the experiment it was possible to secure at will results similar to those obtained by either Dolley or Minnich. It may be noted that Dolley used a filament of a lamp, i.e., a small source and reduced reflection as much as

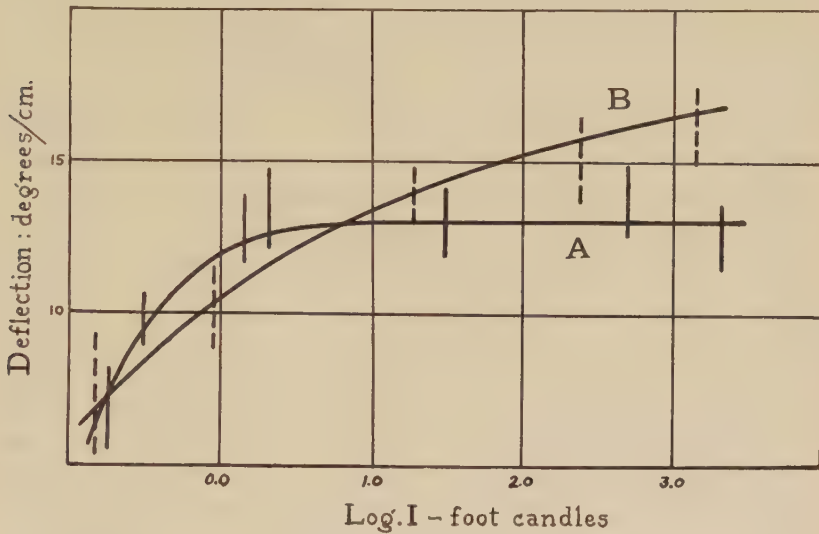


Fig. 2 Curves showing the relation between rate of turning in degrees per centimeter and intensity. Curve A, results when a small source was used; curve B, results when a larger source was used.

possible, while Minnich placed his insects in a compartment the walls of which gave a high reflection from the background. This has been shown above to have the same effect as using a large source. Obviously the difference in results is due to the size of the light source, or to reflection from the background, but these experiments do not show why these modify circus movements. Consequently discussion of this problem will be deferred until observations on these and other factors modifying circus movements have been considered more fully.

MODIFICATION OF CIRCUS MOVEMENTS BY CHANGING THE SIZE
AND LOCATION OF THE STIMULUS IN THE EYE

The stimulus in the eye can be localized in two ways: 1) by covering all parts except those which are to be stimulated, and 2) by using a concentrated source of light so as to produce a definitely localized image on the retina.

Neither one of these methods is ideal for the prosecution of the problem under investigation, namely, the relation between circus movements and localized stimulation. By covering certain parts of the eyes it is possible to make sure that these are not illuminated, but we do not know that all parts of the eyes remaining uncovered are equally stimulated. Moreover, the effect of the covering may be such as to interfere seriously with the reaction to light as shown by Dolley ('16). In localizing the stimulus by means of a concentrated source of light it is difficult to evaluate the effect of the reflection from the background. However, both methods were used, separately or in combination.

An experiment was devised to find the relation between circus movements and different kinds of illumination when different parts of the eye were covered. The upper portion of the right eye of an insect was covered. The insect was dark adapted for 6 to 8 hours, then put on a heavily smoked paper on the platform illuminated by the vertical beam (non-directive light) produced by the apparatus used in the previous experiment and left half a minute, during which time the insect traced all its movements on the smoked paper. Then the black paper was replaced by a white paper and tracings made of the path with a black pencil, requiring about a half minute, after which the white was replaced by black paper and further tracings secured. Then the insect was exposed on black paper in diffuse directive light in front of a window and tracings secured. It was then exposed on black paper in the darkroom in a well-screened beam (directive illumination) from a concentrated source and tracings secured (figs. 3, 4). These tests were repeated with six other specimens with the same portion of the eyes covered, and with forty-four other

specimens with other portions of the eyes covered. A summary of the results obtained in all the tests is presented in table 1.

An analysis of table 1 shows the following:

TABLE 1

Relation between circus movements and the localization of stimulation by
 1) covering various parts of the eye; and 2) controlling the direction of the
 light rays. UR, LR, upper and lower portion of right eye respectively;
 UL, LL, upper and lower portion of left eye respectively.
 X indicates the portion of the eye covered

NUMBER OF INSECTS TESTED	PORTION OF EYES COVERED				NON-DIRECTIVE LIGHT		DIRECTIVE	
	UR	UL	LR	LL	Black back- ground	White back- ground	Diffuse source	Concentra- tion source
6	X				Left	Left	Left	Direct to light
4		X			Right	Right	Right	Direct to light
2				X	Right	Right	Right	Direct to light
5			X		Left	Left	Left	Direct to light
5	X	X			Indif- ferent	Indif- ferent	No turn	Direct to light
3	X		X		Left	Left	Left	Direct to light
4	X			X	Left	Right	Right	Deviates right
6		X	X		Right	Left	Left	Deviates left
6		X		X	Right	Right	Right	Direct to light
3	X	X	X		Right	Right	Right	Direct to light
1		X	X	X	Left	Left	Left	Direct to light
4	X	X		X	Left	Left	Left	Direct to light
1	X		X	X	Right	Right	Right	Direct to light

1. With any portion of either eye covered, the insect performs circus movements toward the uncovered eye in non-directive and diffuse directive light, but moves directly toward the source in well-screened directive illumination.

2. With the upper or the lower portion of both eyes covered, the insect responds as if both eyes were uncovered.

3. With both portions of the eye on one side covered, the insect performs circus movements toward the uncovered eye in non-directive and diffuse directive light, but moves directly toward the source in well-screened directive illumination.

4. With the upper portion of one eye and the lower portion of the other covered, the insect performs circus movements toward the side with the functional upper portion of the eye in non-directive light on a black background, and toward the opposite side on a white background. In well-screened directive illumination, it moves diagonally across the beam in the direction of the functional upper portion of the eye. In diffuse directive light, it performs circus movements toward the side with the functional upper portion of the eye (fig. 3).

5. With the upper portion of both eyes and the lower portion of one eye covered, the insect performs circus movements toward the uncovered portion in non-directive and in diffuse directive light, and moves diagonally across the beam toward the side with the uncovered portion of the eye in well-screened directive illumination.

6. With the lower portion of both eyes and the upper portion of one covered, the insect performs circus movements toward the side with the uncovered upper portion of the eye in non-directive or diffuse directive light, and moves directly toward the source in a well-screened directive beam of light.

Since the insects with the lower portion of one eye and the upper portion of the other covered, perform circus movements toward the side with the uncovered lower portion on a white background, it appears obvious that the direction of circus movements is dependent upon the amount of light entering the lower portion of one eye in relation to the amount entering the upper portion of the other. The lower portion of the eye is largely, if not entirely, illuminated by light reflected from the background while the upper portion is largely, if not entirely, illuminated by light directly from the source. The latter is under all conditions more intense than

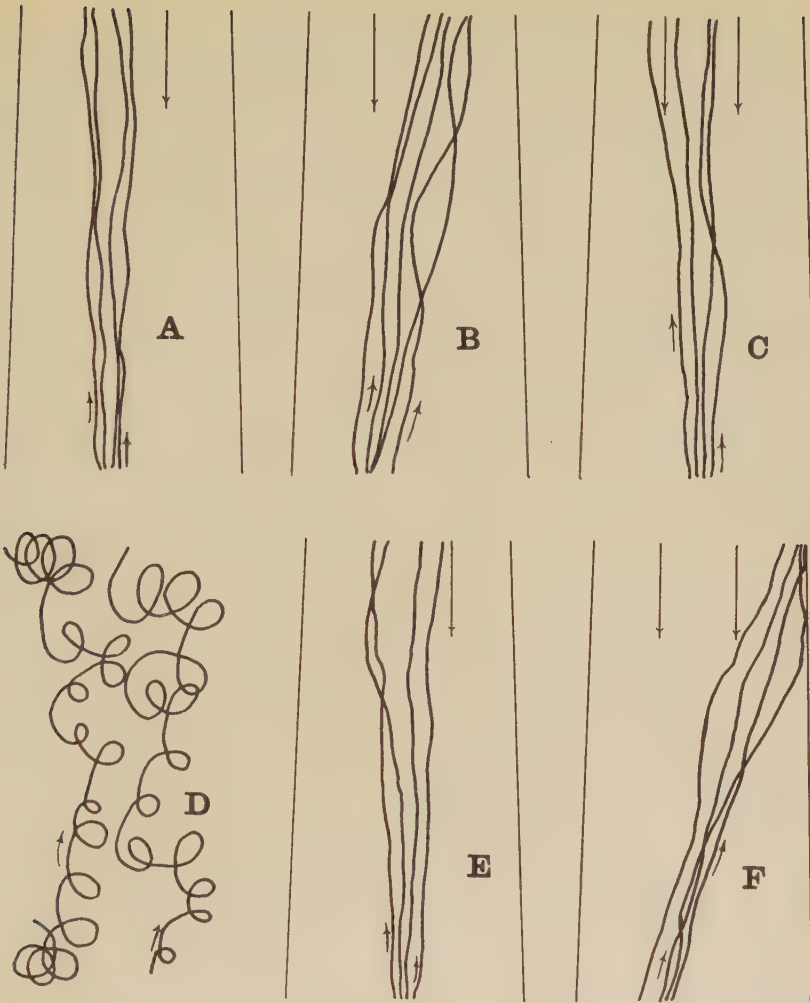


Fig. 3 Paths of *Dineutes* showing effect on orientation of covering different portions of the eyes, A, B, C, E, F, paths in horizontal beam of light from a 500-watt Mazda projection lamp; D, in light from an open window; A, right eye covered; B, upper portion of right and lower portion of left eye covered; C, upper portion of right eye covered; D, upper portion of left eye covered; E, upper portion of right and lower portion of left eye covered; F, only the lower portion of the right eye functional. Large arrows, ray direction; small arrows, direction of locomotion. Each group of paths made by one individual. Heavy lines, boundaries of the beam.

the former. The fact that the insect, in spite of this, turns toward the side with the lower portion of the eye uncovered, i.e., toward the side receiving the less intense light, shows that the lower portion of the eye is more sensitive than the upper or that the stimulating effect of the light received from the background is greater than that of the light received directly from the source.

To ascertain which of these postulates is correct, apparatus was constructed by means of which the insects could be directly illuminated from below, or from above, or from above and below simultaneously.

This apparatus consisted essentially of two 150 watt Mazda lamps, each enclosed in a box with a circular opening 4 cm. in diameter in one end, through which a beam of light passed, and a square glass plate, 40×40 cm. This plate was ruled into 1 cm. squares with very fine lines of India ink. The boxes were mounted 1 meter apart, one above the other in such a manner that the beams were directed toward each other in the same vertical line. The glass plate was mounted between the two boxes 50 cm. from each light so that it intercepted both beams. Wratten neutral tint filters could be inserted across the beams to regulate the intensity. Both lights were screened in the same manner, the openings in the boxes were the same in size, and the beams were in the same vertical line so that the light impinging upon the glass plate from them was the same except in direction. To reduce reflection the whole apparatus was surrounded by black cloth.

The tests were made as follows: The upper portion of the right eye and the lower portion of the left eye of an insect were covered. It was now dark adapted for $\frac{1}{2}$ hour and then exposed on the glass plate in light from above and records ⁴ of its path made. Then it was exposed in light from below, and records of its path again made. Finally, it was simultaneously illuminated from above and below and records of its path secured. This was repeated with a considerable number

⁴ By using the black lines on the glass plate as guide lines, the course of the insect was traced on a sheet of white paper ruled like the plate.

of specimens. The results obtained were essentially the same for all.

When exposed to light from above all the specimens tested made circus movements to the left; when exposed to light from below they made circus movements to the right, and when simultaneously illuminated from above and below with equal intensity there were practically no circus movements.

It appears quite obvious from these results that the upper and the lower portions of the eyes are equally sensitive. When illuminated from above on a white background, insects with the upper portion of the right eye and the lower portion of the left eye covered, turn to the left. If the upper and lower portions of the eyes are equally sensitive, this demonstrates that the reaction must be due to greater stimulation efficiency of the reflected light than of the light received directly from the source. This result must be due to difference between the size of the reflecting surface and that of the source of light, the former being much larger than the latter.

In order to ascertain more specifically the relation between the size of the source of light and stimulating efficiency, the apparatus was modified by placing a ground glass plate in front of each lamp to act as a secondary source of light. The distance of each lamp from the glass plate upon which the insects were exposed was adjusted so that the intensity of light falling upon it from above was equal to that falling upon it from below when the areas of the secondary sources were equal. The intensity of the light, either from above or from below, could be changed by changing the area of the secondary source. It was also possible to change the intensity of the light by placing Wratten neutral tint filters across the beam. For example, by doubling the area of the secondary source of light, the intensity of light could be doubled, but if, at the same time, a 50 per cent transmission Wratten neutral tint filter was placed across the beam, the intensity was the same as before although the area of the secondary source was changed. Consequently by using suitable combinations of Wratten filters and screens to limit the size of

the secondary source, it was possible to secure a series of beams with different sizes of secondary sources but equal in intensity.

The experiments were carried out with the intensities of the light received from the two secondary sources constant and equal, and with the lower secondary source constant in size but with the upper secondary source varying in size. The insects were tested in the same manner as in the preceding experiment, except that they were tested before and after the portions of the eyes were covered, and only in a field of light produced by simultaneous illumination from above and below. Records, made as described above, were secured of the paths, some of which are represented in figure 4. The circus movements were measured by deflection in degrees per centimeter of path. The results obtained are presented in table 2.

These results show that the normal insects turned indifferently to the right and the left regardless of changes in the size of the secondary sources of light, and that the angular deflection in their paths was nearly the same in all tests. They also show that when the areas of the secondary light sources are equal the insects, with their eyes covered as described, turn indifferently to the right and the left and their angular deflection per centimeter is nearly the same as in normal animals. But they show that if the ratio of the area of the upper source of light to that of the lower is more than 1, they turn to the left (toward the functional portion of the upper eye); and if less than 1, they turn toward the right (toward the functional portion of the lower eye). It will also be seen that as the ratio becomes greater than 1 or less than 1, the angular deviation per centimeter increases.

The results of the experiments described above demonstrate that the size of the source of stimulation in vertical illumination is closely correlated with the rate of turning in circus movements. It was thought that possibly a similar correlation exists in circus movements performed in a horizontal beam. If this is true, it may offer an explanation of the diverse results obtained by other investigators.

Experiments designed to test the validity of this notion were made as follows: A specimen of *Dineutes* whose eye on one side had been covered was dark adapted for 2 hours. It was then exposed on black paper in a well-screened horizontal beam of light and tracings made of its path; then a piece

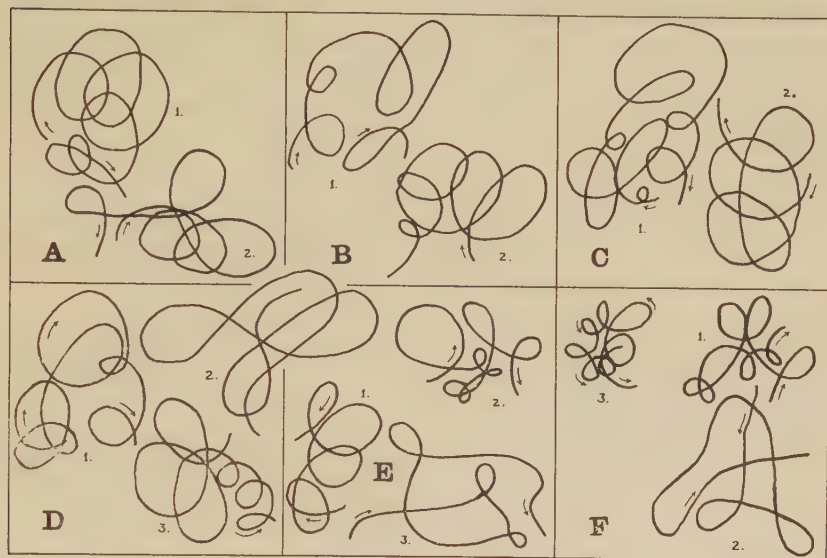


Fig. 4 Paths showing, in non-directive illumination, response of *Dineutes* with different portions of the eyes covered. A, light from above, upper portion of left eye covered; 1, path on a white background; 2, path on a black background. B, light from above, lower portion of left eye covered; 1, path on a black background; 2, path on a white background. C, light from above, left eye covered; 1, on white background; 2, on a black background. D, light from above; 2, path made by specimen with both eyes functional; 1, specimen with upper portion of left and lower portion of right eye covered on black background; and 3, on white background. E, eyes covered as in D, but 1, light from above; 2, light from below; 3, light from above and below. F, eyes covered as in E; light from above and below equal in intensity. 1, area of upper light, 15 sq.cm., lower light, 0.5 sq.cm.; 2, upper and lower lights equal in area; 3, area of light from above, 0.5 sq.cm., from below 50 sq.cm.

Note that if the lower portion of one eye and the upper portion of the other is covered, circus movements are made toward the functional upper portion of the eye on a black background and in the opposite direction on a white background. Moreover, in light from above and below, circus movements are made toward the functional upper portion of the eye if the area of the upper light source is the greater, toward the opposite side if less, or they tend to disappear if the areas and intensities of the two lights are equal.

of white cardboard, 1×1 cm. was placed 300 cm. behind the insect and in the center of the beam with the flat surface perpendicular to the rays of light. Tracings were then made of the paths and a record kept of the number of trips necessary to eliminate circus movements completely. The test was repeated with cardboard 2×2 cm. and then with cardboard 5×5 cm. Then it was repeated with other specimens, the distance between the cardboards and the insects being varied in some cases. A summary of the results is given in table 3.

TABLE 2

Rate of turning and direction of circus movements in specimens of Dineutes with the upper right and lower left portion of the eyes covered as related to the areas of the upper and lower light sources. Intensity of upper and lower lights equal. Rate of turning measured by deviation in degrees per centimeter

NUMBER OF INSECTS TESTED	AREA OF SOURCE OF LIGHT (U) FROM ABOVE IN SQUARE CENTIMETERS	AREA OF SOURCE OF LIGHT (L) FROM BELOW IN SQUARE CENTIMETERS	RATIO $\frac{U}{L}$	DIRECTION OF CIRCUS MOVEMENTS		AVERAGE DEVIATION IN DEGREES PER CENTIMETER	
				Normal	Insects with portion of eyes covered	Normal	Insects with portion of eyes covered
8	25	1	25	Indifferent	Left	5.2	11
5	10	1	10	Indifferent	Left	6.3	11.5
6	2.5	1	2.5	Indifferent	Left	6	10
3	1	1	1	Indifferent	Indifferent	6.4	6
8	0.25	1	0.25	Indifferent	Right	5.5	11
2	0.025	1	0.025	Indifferent	Right	7	11.75

By referring to this table it will be seen that depending upon the size of the reflecting surface and upon its distance, insects may go directly toward the source; may perform circus movements for a few moments and then go directly toward the source; may perform circus movements for a long time and then take a path diagonally across the beam, or may perform circus movements continuously.

It should be noted that the first and the third of these results are similar to those obtained in a well-screened directive and in a diffuse directive illumination, respectively. This shows that the difference between the response of *Dineutes* in diffuse directive and well-screened directive il-

lumination is due to differences in the light reflected from the background.

Similarly, it should be noted that the results presented above for *Dineutes* are much like those obtained by investi-

TABLE 3

Modification of reactions of insects blinded on one side, produced by changes of the background

NUMBER OF ANIMALS TESTED	REACTION IN BEAM ALONE	REACTION IN BEAM AND REFLECTED LIGHT					
		Background no. 1 (1 sq.cm.)		Background no. 2 (4 sq.cm.)		Background no. 3 (25 sq.cm.)	
		Distance from animal in centimeters	Reaction	Distance from animal in centimeters	Reaction	Distance from animal in centimeters	Reaction
4	Went directly toward source	300	Went directly toward source	300	Movement toward course; occasional circus movement	10	Circus movements continuously
6	Went directly toward source	200	Went directly toward source	200	Occasional circus movements		
3	Went directly toward source	50	Circus movements but eliminated them after 4 trips	50	Circus movements eliminated after 36 trips, then diagonally across beam		
3	Went directly toward source	10	Circus movements eliminated after 24 trips	10	Circus movements continuously		

gators working with other insects. Carpenter ('05) maintains that *Drosophila* with one eye covered went directly toward the source of light; Holmes ('05), Dolley ('16), Minnich ('19) and Mast ('23) observed in various other insects that while there were circus movements with one eye covered

they soon disappeared in a well-screened horizontal beam, and Dolley (*loc. cit.*), Minnich (*loc. cit.*) and Mast (*loc. cit.*) found that in the insects they studied, circus movements persisted in diffuse directive illumination. Therefore, it seems obvious that the different results secured by these authors are largely, if not entirely, due to differences in the light reflected from the background or to differences in the size or position of the light source.

DISCUSSION

From the foregoing experiments it is obvious that specimens of *Dineutes* react in a number of different ways depending upon the conditions under which they are exposed. It is impossible to show that any single type of reaction is the fundamental one, for each is unique under the particular conditions calling it forth. Any theory of orientation, to be adequate, must take into account all the reactions demonstrated here experimentally.

Various theories have been advanced to explain the orientation of insects to light. A number of them, e.g., ray direction (Sachs, 1876); volition (Romanes, 1883); molecular polarization (Bohn, '20); have aroused no recent interest. Present day investigators are inclined to accept either the tropism theory of Loeb, or the "differential response to localized stimulation" theory of Mast.

Following are the essentials of Loeb's tropism theory formulated in his last work on the subject ('18):

1. Symmetrically located regions on the surface of an animal are chemically identical.
2. Light brings about a stationary process in the elements of the eyes, in which the mass of the reaction products is determined by the Bunsen-Roscoe law.
3. In proportion to this photo-chemical mass action, corresponding chemical reactions take place in the brain elements with which the eyes are connected.
4. As a consequence, corresponding chemical reactions take place in the muscles by which the tension of the latter and

through this, the size of the steps is determined (Loeb, '18; p. 21 footnote).

5. The light impinging on one eye through the above processes causes the legs on the same side to become more flexed and those of the other side to become more extended, and the amount of flexion and extension is proportional to the intensity of the light.

Loeb's tropism theory seems to be in accord with the following facts:

1. Insects blinded in one eye perform circus movements continuously in illumination from above, in horizontal illumination from a large source, and in horizontal illumination from a small source, if the reflection from the background is large.

2. The rate of turning increases with increase of intensity if the source of illumination is large or the amount of reflected light is high.

His theory is, however, unable to explain the following facts:

1. In *Dineutes* with one eye covered, the rate of turning toward the functional eye in vertical illumination from a small source of light, does not increase with increase in intensity, if the intensity is higher than 1.3-foot candles.

2. Under certain conditions *Dineutes* and a considerable number of other species of photopositive insects, perhaps all, still orient after one eye is covered and then go fairly directly toward the light.

3. Under certain conditions, *Dineutes* and probably all insects which are photopositive perform circus movements for a time and then eliminate them.⁵

4. The rate of turning toward the functional eye depends upon the size of the source of light if the intensity remains constant.

⁵Loeb apparently did not recognize such responses. But some of his followers who did, notably Minnich, still believe that the response of insects to light is fundamentally in accord with the Loeb tropism theory. They explain the observed inconsistencies by assuming that learning by experience modifies the expected results. It was shown (Clark, '28) that it is not necessary or even possible to evoke the aid of experience to explain such reactions.

5. The stimulating efficiency of light varies directly with the size of the source of light.⁶

To account for all the facts of orientation in so far as they were known, Mast ('23, '24) formulated the following assumptions, most of which are strongly supported by well-established facts.

1. The stimulating efficiency of light depends upon the location of the image on the eye of insects; the further back the higher the efficiency, i.e., the more sensitive the retina.

2. The orienting response is a reflex or a chain of reflexes.

3. The character of these reflexes depends upon the location of the stimulus in the eye.⁷

4. Stimulation in either eye affects the direction of movement of the legs on both sides.

5. Turning is primarily due to the direction of movement of the feet on both sides and only secondarily to difference in the length of the steps on opposite sides.

6. The response to stimulation of a given region in one eye is modified by simultaneous stimulation of the same or different region in the other eye.

These assumptions account for all the facts in hand except three, namely: 1) the elimination of circus movements after exposure to light for some time, 2) the variation of stimulating efficiency with the size of the source of stimulation, and, 3) the increase in deflection in vertical illumination as the intensity increases from 0 to 1.3-foot candles, if the source of light is small, and over a wider range if the source is large or if there is considerable reflection from the background.

To account for these facts the following additional assumptions are formulated:

1. Each ommatidium follows the 'all-or-none' principle. There is some evidence that this is true for the rods in the

⁶ Several other facts presenting serious objections to Loeb's theory are presented by Mast ('23, p. 185).

⁷ If only the inner ommatidia of one eye are stimulated, a positive insect turns toward the unstimulated eye; if the anterior ommatidia are stimulated no turning occurs, and if the outer lateral ommatidia are stimulated the insect turns toward the stimulated eye.

human eye (Ives, '22); and according to Parsons ('25) rod vision is crude, vague, undifferentiated, and perhaps more primitive in character than cone vision. If this is true, it is reasonable to assume that the receptors in more primitive forms behave somewhat like rods.

2. The thresholds of the ommatidia vary in such a manner as to give approximately a normal distribution curve. This postulation has been used successfully by Hecht ('28) in his theory of human visual acuity and by Hecht and Wolfe ('29) in their work on the honey-bee.

3. The larger the number of ommatidia stimulated, the greater the reaction. Clark ('33) has shown this to be true for retinal potentials in the excised compound eye of *Limulus*.

4. Light brings about a stationary state in the photo-sensitive elements in the eyes; thus the sensitivity and the threshold of the receptors are dependent upon the light to which they have been exposed. As yet there has been no adequate study of the threshold values at different levels of light adaptation in insects, so a more exact formulation must await investigation.

Let us now attempt to explain the three facts under consideration:

1. If an insect with one eye blinded is exposed to light, some of the ommatidia receive light directly from the source and others receive light reflected from the background. If the source is above, the anterior, the posterior, and the lateral ommatidia receive essentially the same amount of light no matter in which direction the insect faces, and since the posterior ommatidia are more sensitive than the anterior (Mast, '23) it continuously turns toward the side containing the functional eye. If the beam is horizontal, the source small, and the reflection from the background so weak that its intensity is below the threshold of the lateral and the posterior ommatidia; and if stimulation of the anterior ommatidia induces reflexes which result in straight forward movement (Mast, '23) the insect turns until it faces the light and then proceeds directly toward it. This accounts for the orientation

of insects with one eye blinded. If the intensity of the reflection from the background is not below the threshold of the posterior and lateral ommatidia, the insect turns toward the functional eye until, owing to adaptation, the threshold of the posterior and lateral ommatidia is raised above the intensity of the reflected light and then proceeds directly toward the source of light (Clark, '28). This explains the elimination of circus movements. The responses to rapid changes of intensity of insects oriented diagonally in a beam of light can be explained on the same basis (Clark, '30).

2. It is obvious that the number of ommatidia stimulated varies directly with the size of the source of light and that if the 'all-or-none' principle holds, the magnitude of stimulation is directly proportional to the number of ommatidia stimulated. The stimulating efficiency, therefore, varies directly with the size of the source provided the intensity is continuously above the threshold of all the ommatidia involved. Our postulates therefore explain the fact that the stimulating efficiency varies directly with the size of the source of light.

3. If the source of light is small and is above the insect, a few ommatidia on the upper surface of the eye receive light directly from the source and some on the posterior, the lateral, and the anterior surfaces receive light reflected from the background. If the intensity of the reflected light is continuously below the threshold of the ommatidia illuminated by it, the ommatidia on the upper surface are the only ones involved in stimulation. If now the intensity of the source is increased, the intensity first exceeds the threshold of the most sensitive ommatidia and then that of more and more of the less sensitive ones until it exceeds the threshold of all, and all are stimulated, after which there is no further increase in the magnitude of stimulation, no matter how much the intensity is increased. If this is true, an insect with only one functional eye, on a non-reflecting background illuminated with light from a small source above should, as the intensity of the light increases, turn more and more sharply toward the functional

eye, until a certain intensity is attained, after which there should be no further increase in the rate of turning.

If the intensity of the reflection of the light from the background is above the threshold of the ommatidia illuminated by it, the same should occur, but since the reflected light is lower in intensity than the direct light, increase in turning should not cease until a higher intensity of the direct illumination is attained.

If the source of light is large there should also be increase in turning as the light increases, but the increase in turning should not cease until the intensity attained is higher than that which obtains for a small source; for with a large source the light is spread over a larger area, so that for any given intensity each ommatidium in this area receives less light than it does when the insect is illuminated with light from a small source.

All this is precisely what was observed in *Dineutes*. The assumptions, therefore, account for the facts under consideration.

SUMMARY

1. Dineutes blinded in one eye performs circus movements continuously if the source of light is large, and the reflection from the background fairly strong, regardless of the direction of illumination.

2. It performs circus movements for a time and then eliminates them, if the source of light is not so large and there is but little reflection from the background.

3. It performs no circus movements if the beam is horizontal, the source small, and the reflection from the background weak.

4. In vertical illumination deflection toward the functional eye increases as the intensity of light increases over any portion of the range from 0 to 1.3-foot candles, if the source of light is small, and over a wider range if the source is large or if there is considerable reflection from the background.

5. The magnitude of the response varies directly with the size of the source of light.

6. If certain assumptions are added, the differential 'response to localized stimulation' theory of Mast explains the results presented in this paper.

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